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Cornell University
complements of

W. A. COBB,

Tylenchus and Root-gall.

(With twenty original figures, on wood, drawn with the camera lucida.)

By N. A. COBB.

I.

LIFE HISTORY OF TYLENCHUS ARENARIUS.

To the Director of Agriculture.

Sir,

I send you a small potato showing a disease or parasite that affects the skin. It comes in small knobs at first, and gradually spreads over the potato. I think it is some insect in the ground, as it comes on the roots of the potato first, like knots on a stout thread. On about an acre and a half of ground I sowed two bags of lime and one bag of salt, but it had no effect. It has been in my paddock for the past four or five years, and is constantly growing worse. It affects parsnips, mangels, and the roots of the peach trees, and I have seen it on the roots of large Swede turnips; and I am inclined to think it kills the newly sown turnip. I have sown turnips three times since February; after coming through the ground they gradually grow yellow and die off. The last time I dusted them with lime just after they broke the ground, but it did no good; they died off like the rest. My soil is rich scrub land, and I manure it well. It has been under crop for the last twelve or fourteen years. If there is any practical remedy will you oblige by letting me know at your earliest convenience. I enclose some of the soil with the potato.

Yours respectfully,

WILLIAM EASSON.

In accordance with Mr. Easson's suggestion that it was an insect pest that was giving him so much trouble, the specimens accompanying the foregoing letter were forwarded to the Consulting Entomologist of the Department, who reported that the disease was certainly not due to the attack of any insect. The specimen was therefore forwarded to me. After a short examination I wrote to the Director of Agriculture that although the specimen was not such as to permit me to say with certainty, yet from what I could discover, and from Mr. Easson's description of the manner in which his various crops were affected, I had little doubt that his land was infested with a destructive Nematode worm, similar to that which has proved so disastrous to the sugar-beet crop in Europe, and that if my suspicion was correct, it was important that the matter be at once and thoroughly investigated; and concluded by desiring that further specimens, both of various diseased roots and of surface and sub-soils, should be forwarded to me for further examination.

In accordance with my request Mr. Easson forwarded various samples, as will be seen by reading the following letter:—

To the Director of Agriculture.

Sir,

I have sent by this mail two packets containing samples of soil and roots—potato, parsnip, and peach-tree roots. The disease can be clearly seen on the parsnip and potato, and a little on the peach-tree roots. I have seen it much thicker on peach-tree roots than on the sample. The potato is taken from four drills planted about Christmas. They were well dunged with pig-sty manure. The potato was planted on the dung, then covered, then a bag of lime sown on the top in the drills, then covered over again. The four drills were about 200 yards long, so I think they had a fair trial of lime; but it had

no effect in checking the disease. The longer the potato is left in the ground the worse it gets. The disease seems to be most active in summer. You will scarcely see it in the late crop of potatoes. It affects mangels, parsnips, and potatoes worst. It does not seem to trouble carrots or the roots of orange-trees. I have had to give up growing mangels the past three years on account of the disease. The soil is naturally well drained, and a depth of sub-soil sent up to 40 feet. The insect or disease seems to live in the soil.

If any other information or samples are required, I will promptly attend to it.

Your obedient servant,

WILLIAM EASSON.

I devoted three days to a further partial examination of the Pretty Gully Scrub disease, and was confirmed in my first suspicion, namely, that the roots were attacked by a microscopic Nematode worm infesting the soil. The results of my examination were outlined in conversation with the Director of Agriculture, who at once saw the importance of carefully investigating the disease. The examination I had made was but very incomplete, and I was cautious about making any broad statements concerning a disease so superficially examined, and when, soon after, I was desired to make a written report upon the disease, I consented to do so, with the understanding that it should be regarded as in every sense preliminary. Any opinions based on such imperfect investigation as I have barely found time to make, must of course be subject to revision when the life-history of the pest has been carefully followed through at least one entire year. I must add that much of the investigation lies on the very verge of what can be accomplished with the microscope of the present day, and furthermore, would be found impossible by anyone not already familiar with the free-living Nematodes—facts which will be constantly emphasized even in this preliminary report. I have been made more willing to prepare this imperfect account by representations setting forth that it was desirable to make known to the public the nature of the work coming properly within the scope of an Agricultural Department, an argument whose weight is obvious.

The Disease.

I have not visited any Australian district infested by the disease under discussion. For the manner and time of its appearance, the reader is referred to Mr. Easson's letters. As I shall soon point out, the disease is caused by microscopic worms which pass certain stages of their existence in the tissues of roots, there giving rise to the most obvious symptoms. When the disease first appears, small galls of various shapes begin to form on the roots at the points of attack. These galls when occurring on a rootlet have been appropriately compared to knots tied in a stout thread. When they occur on the roots, they take on the form of more or less irregular excrescences of various sizes up to a diameter of half an inch. If the plant is young when first attacked, its leaves gradually become yellow, it droops and soon dies. The time occupied by these changes varies with the nature of the plant. Mangels and turnips die in a few weeks. Young trees on the other hand withstand the disease for from one to two years, their vitality steadily decreasing until at last their leaves drop and they show no further signs of life. Upon examination the roots are found to be covered with galls. The characteristic appearances produced by the disease are sufficiently illustrated by the plate at the end of this report. The plate represents, among other things, a parsnip forwarded from Pretty Gully Scrub by Mr. Easson. The upper rootlets are completely covered with small galls, and larger galls are to be seen on the tap-root near its end, as well as on the large lower root on the right. Here and there appear large excrescences or warts, also due to the attacks of the worm. The plate also represents a potato sent from

Pretty Gully Scrub. Its appearance is not easily described. It was completely covered with knobs, some smooth, others rough and warty. These knobs varied from the size of a pin's head to that of a bean. When smooth, as were most of the smaller knobs, they had a water-soaked appearance, and cutting them only confirmed the impression gained from outward inspection. It is this water-soaked appearance which sometimes gives to the smoother knobs the aspect of blisters. The potato shown in the figure weighed $2\frac{1}{4}$ ounces, and I estimated it to contain upwards of 10,000 mature, or nearly mature, worms, and a much larger number of younger worms and innumerable eggs.

The only other roots forwarded from Pretty Gully were those of the peach-tree. The appearance of the disease as manifested in peach-tree roots is also shown by the plate.

From what I have learned of the habits of similar parasites, I suspect that the Pretty Gully Scrub worm will be found, upon more careful search, to infest, to a greater or less extent, nearly every cultivated plant and many wild ones.

Methods of Examining.

In searching for the worms, not all roots are equally easy to examine. The tissues of the parsnip, for example, are so tough that as a rule many worms will be mutilated in the endeavour to extract them. The same is true, to a certain extent, of peach-tree roots. The tissues of potato yield up the worms more readily. The method used most successfully in extracting both mature and young worms, was the following:—Cut from the potato slices one-eighth of an inch thick, and place them in water in a shallow glass dish. On examining with a magnifying glass the mature worms will appear as white sacs of the size of a pin's head. If the worms are numerous, some of them will be seen to have been cut in two, giving rise thereby to a milkiness. Search for one which remains uninjured, and, using transmitted light, cut it away from the slice in a cube of the tissue just large enough to contain it. The operation should be performed with a small sharp knife. The cube will be sufficiently translucent to give a rather indefinite view of the worm. Now with a pair of exceedingly sharp needles gradually and carefully remove the tissue bit by bit. After some minutes, if no slip be made, the worm will fall out from the cavity which contained it. Any slip or the slightest pressure will burst the worm and render it comparatively worthless for purposes of examination. The worms first removed will probably have the form shown in II, Fig. 1, on the following page, and it is to the structure of this form that we will turn our attention, after first noting the methods by which we shall obtain the best results.

For immediate examination the worm is best placed in $\frac{1}{6}$ per cent. osmic acid. Examination in water is much less satisfactory. The best method of all is to kill at once in warm concentrated solution of corrosive sublimate, and then bring the specimen, by means of the differentiator, into balsam, after having stained with Mayer's carmine. Borax carmine does not penetrate the cuticle sufficiently to stain the tissue, at least in a reasonable length of time. The examination, which of course is microscopic, must be conducted by mounting the worm on an object glass under a cover-slip, supported by two pieces of bristle. The pieces of bristle, or whatever other objects be substituted for them, should have a diameter barely less than that of the worm itself. This permits the cover-slip to press *very slightly* on the worm, and it will be found that by moving the cover the worm can be rolled into any desired position.

Structure of the Worm.

The worm is at once seen to be irregularly flask-shaped, the neck of the worm corresponding also to the neck of the flask. In other words, the large spherical portion is the posterior part of the animal, and the narrow and more or less curved portion is the anterior part. The anterior part terminates in a narrow head, presenting an opening, the mouth. The posterior part, or abdomen as we may call it for the present, terminates at its extreme posterior point, *v*, Fig. 1, in a large opening, which is not the anus, as might be expected, but the vulva or sexual opening. The outer covering of the worm consists of a transversely-striated transparent cuticle, the striae being most clearly visible in the neighbourhood of the head. The mouth-opening is surrounded by three very obscure lips, behind which is a mouth-cavity containing a characteristic spear. This spear, which terminates posteriorly in three knobs and is capable of being thrust forth and withdrawn, usually lies with its point slightly behind the lips. Leaving the mouth cavity, the food passes through a chitinous tube into a prolate, highly muscular bulb and thence through a short tube it passes into the intestine, if such still exist. (As will be explained farther on, the intestine has a remarkable way of disintegrating.) The dimensions of the above-mentioned organs are as follows:—Taken as a whole

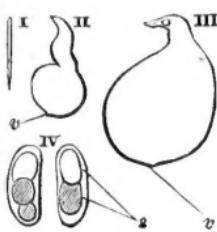


FIG. 1.—GALL-WORM
(*T. arenarius*).

I, II, and III, successive stages in the growth of the worm $\times 25$; IV, first two stages, in segmentation of the egg $\times 100$; *v*, vulva or sexual opening; *s*, segments of the egg.

they occupy about one-sixth the length of the entire worm, and constitute the œsophagus. Of the entire length of the œsophagus one-fourth is taken up by the median bulb, one-twelfth by the spear, one-sixth by the portion behind the bulb, and the remainder by the chitinous tube which leads from the mouth cavity to the bulb.

Further examination discloses other interesting points, but we must postpone their consideration until we have examined the young worm from which this sac-like, flask-shaped form has originated. This course will lead us through a series of researches which it is not worth while to detail in full. Suffice it to say that, on returning to the slice of potato, smaller specimens than that just described will be discovered, this discovery will be followed by finding yet smaller ones, and so on until we arrive, step by step, at the conclusion that the large flask-shaped worm entered the potato as an exceedingly small worm of a *totally different shape*. A search in the soil, if conducted in a proper manner, soon discovers this minute worm,—that is, the young or larva of the adult flask-shaped form.

The larvae as taken from the soil present themselves as slow-moving, transparent worms of the form shown in I Figs. 1 and 2, and have the following dimensions: * $\frac{3.2}{2.4} \frac{15}{3.3} \frac{17.6}{3.4} \frac{M}{3.6} \frac{87.9}{2.3} .45$ mm. The cuticula is devoid of hairs and is traversed by about 500 transverse striae. The neck is cylindroid to opposite the base of the buccal cavity, but thence to the mouth convex-conoid. There are no cephalic setæ, and but the faintest indications of a lip region. There are no definite organs of vision, and apparently no lateral organs. The spear, which is three-bulbed at its base, is generally drawn back so that its point is removed half the spear-length from the mouth. (See II Fig. 2.) That portion of the œsophagus in front of the median bulb is narrow but of rather uncertain width, and is lined throughout with thick chitinous

* For the dimensions the reader will please give preference to the formula, I Fig. 2 being considerably too wide though otherwise correct. For an explanation of the formula see page 131, Vol. I, Part 1.

walls. The ellipsoidal median bulb is situated just in front of the somewhat oblique nerve-ring and is connected with the smaller and weaker posterior bulb or swelling by a canal one-sixth as wide as the adjacent portion of the neck. While the median bulb and all of the oesophagus in front of it are characterized by possessing a thick, transparent, horny lining of the same composition as the spear, the posterior portions of the oesophagus are nearly devoid of such linings. If, therefore, the oesophagus be divided by a transverse cut just behind the median bulb it is separated into two dissimilar parts, of which the anterior is the stouter and better developed. The pellucid alimentary canal is two-thirds as wide as the body, and its cells are closely packed with coarse spherical granules. The unicellular ventral gland empties, by means of a long chitinous duct, through the porous excretorius just opposite the commencement of the intestine. The lateral fields are one-fourth as wide as the body and have a double structure, presenting four parallel longitudinal lines. The tail is conical from the inconspicuous anus. There are no caudal glands, and the terminus is pointed.

From this description it is evident that, so far as the larvae are concerned, this worm must be referred to the genus *Tylenchus*, and it may as well here be added that the adult form presents no features that alter the decision thus made from the structure of the larva.

We have now to trace the development of the larvae. I have found the larvae in the soil sent from Pretty Gully Scrub. That they are abundant in the soil there is beyond doubt. I found them in the first particle examined, but have not made sufficiently careful search to be able to give a precise notion of their exact abundance. It is here to be noted that the soils examined were forwarded by mail, reaching my private laboratory after being several days on the way, and when finally examined were quite dry and caked. It is certain that the larvae can endure a short desiccation, for those contained in this soil revived on being placed in water, and furnished the specimens from which the foregoing description was taken. This ability to withstand drying is a characteristic of many Nematode species. The young of some species revive after being kept in a dried-up state for several years. This fact will be referred to again in speaking of contagion.

It is necessary to assume that the larvae make their way into young roots at an early stage of their existence. How long they may live in moist soil without entering roots of living plants I am unable to say. It is not impossible that it may be a long time, but for two reasons it is improbable. First, I have found no specimens living free in the soil that measured above '54 millimetres, but have on the other hand found specimens inside the tissues of roots that measured not more than that, although the diameter was relatively greater than in the free-living larvae. Such a specimen is shown in Fig. 3. Its dimensions were as follows: $\frac{12}{3.5} \frac{21}{4.5} \frac{17.9}{2.5} \frac{M}{16.1} \frac{9.1}{6}$. '42 mm. Secondly, the entrance into root tissues is accomplished at an early age in an allied species.

The mechanism by means of which the larvae make their way into the roots and rootlets of plants, namely the spear and the median oesophageal bulb,

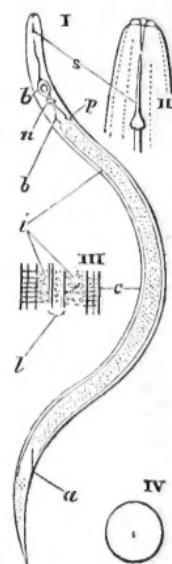


FIG. 2. *T. arenarius*.

I, the larva $\times 200$; II, head of same $\times 900$; III, bit of the middle of the body $\times 600$; IV shows at the centre the actual length of the worm; *s*, the spear; *b*, the bulbs; *n*, the nerve-ring; *i*, the intestine; *c*, cuticle; *l*, lateral fields; *a*, anus.

are shown in the figures, and their structure has already been commented upon. The larva makes its way to a rootlet, applies its mouth, and exerts a powerful suction by means of the muscular median bulb, at the same time thrusting forth its spear by means of appropriate muscles. The cells of the epidermis of the rootlet are thus pierced, and are then sucked dry and made to collapse. At the aperture thus made other and deeper cells are similarly attacked. Continuing this line of action, the worm makes its way into the interior of the rootlet. At least, such I believe to be the method of attack, although I must add that my opinion is deduced from the structure of the organs of the worm and the effects on the tissues of the plant. I have not witnessed the actual entrance of a larva into a rootlet. Once within the rootlet, the worm is in the presence of an abundance of food, and begins to grow apace. Here again it brings into play its piercing and sucking apparatus. Its very existence depends upon these organs, and their importance is attested by the fact that throughout the life of the worm they remain in perfect condition, although numerous other organs become completely degenerate. By continually thrusting forth the sharp spear the juicy cells of the rootlet are pierced, and their contents are then sucked in. The growth of the larvae consists in a rapid and great increase in diameter, so that the originally slender worm soon takes on the plump form shown in Fig. 3. The tail and head alone retain somewhat of their original size and form. Even the tail disappears at a later stage.

Whether the change now to be described takes place at the first moult, I cannot say. Reasoning from the size of the larva, I should answer in the affirmative. It is certain that at an early stage, shown in Fig. 4, the worm undergoes a change in which the tail disappears and, apparently, *the anus with it*. Fig. 4 represents then, we will say, the first or second moult.

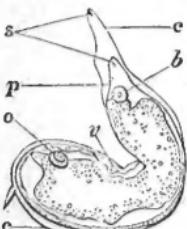


FIG. 4.—MOULTING LARVA OF *T. avenarius*. $\times 100$.
c, old skin; s, spear; v, ventral gland which emptied through excretory pore *p*; b, median bulb; o, rudimentary sexual organ.

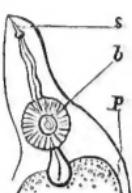


FIG. 5.—NECK AND HEAD OF FIG. 3. $\times 200$.
s, spear; b, median bulb; p, excretory pore.

structure has increased in size, and, therefore, in effectiveness.

Up to this time the sexes remain indistinguishable or nearly so, but at this stage the life-histories of the two sexes begin plainly to diverge, and present, from a biological point of view, a most interesting series of phenomena. Let us first consider the history of the female. Fig. 4 represents a female, the first clear indication of the sexual organs being exhibited in the single cell at *o*. This cell, by dividing, soon gives rise to

a two-parted sexual system—consisting of a vagina, two uteri, and two ovaries,—which grows to such an extent as finally to occupy the greater part of the body. The complete history of its development I have not yet been able to follow, simply from lack of time. I think it presents no unusual difficulties. At the same time that the sexual organs are growing so vigorously other parts of the organism are pursuing an opposite course. As already pointed out, the anus disappears at the first or second moult. Soon all of that portion of the elementary canal behind the oesophagus undergoes a degeneration and disappears. The spear and oesophagus alone remain intact. The muscular layer lining the cuticula also disintegrates. We have, as the result of this growth on the one hand and degeneration on the other, a sac consisting of the cuticula of the worm, almost completely filled with a two-parted egg-producing apparatus, and supplied with nourishment by means of powerful sucking-organs.

If now we turn our attention to the development of the male we find a very different history. No one would have ventured to predict such a remarkable series of changes as we have now to follow. A parallel case is known but for a single animal species, the closely allied *Heterodera (Tylenchus) Schachtii*, Schmidt. As before remarked, up to the stage represented in Fig. 3, the sexes are with difficulty distinguished from each other. But thereafter the history of the male is totally different from that of the female. If the larva shown in Fig. 3 be a male, its next moult gives rise to a slender worm of the form shown in I, Fig. 6. This remarkable moulting condition is shown in III, Fig. 6, where the slender young male is represented as several times coiled inside its former skin of very different shape. By its constant activity it at last succeeds in rupturing the old skin—not, however, before it has again moulted—and issues a distinct male with all the sexual organs complete.

In this condition, which is the adult male state, measurements give the following formula: $\frac{1 \cdot 88}{1 \cdot 2} \frac{88}{2 \cdot 2} \frac{13}{2 \cdot 3} \frac{M \cdot 987}{3 \cdot 16} 1 \cdot 33$ mm., in which 8·8 is the measurement to the centre of the median bulb, inasmuch as I have not been able to satisfy myself as to the exact position occupied by the nerve-ring. The cuticula, like that of the female, is devoid of hairs and presents about five hundred transverse striae. The conoid neck terminates in a truncated head bearing no cephalic setæ, but armed with six distinct, rather hemispherical or conoid lips. I could discover on the only two specimens examined no papillæ, lateral organs or eye-spots. The spear is rather stout for its length, being, no doubt, a very effective organ. That portion of the oesophagus in front of the powerful prolate or ellipsoidal median bulb is one-fourth as wide as the neck and is lined with thick, glistening, chitinous walls. The median bulb itself is two-thirds as wide as the adjacent part of the neck and also presents a chitinous lining in the form of a central apparatus one-fifth as wide as the bulb and of the same form. The intestine is at least two-thirds as wide as the body and its cells are packed with fine granules; it terminates posteriorly in a rectum twice as long as the anal diameter. The tail is obliquely hemispherical-conoid and

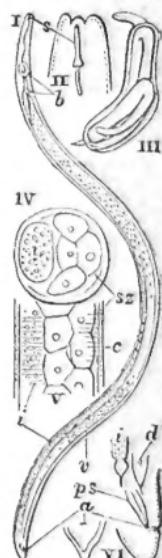


FIG. 6.—MALE OF GALL-WORM (*T. arenarius*).

- I, mature male, $\times 65$;
- II, head of same, $\times 450$;
- III, larval male, inside of its cast off skin, $\times 50$;
- IV and V, cross and longitudinal sections, $\times 350$;
- VI, lateral and ventral view of tail, $\times 225$;
- s*, spear;
- b*, bulbs;
- t*, intestine;
- sz*, spermatozoa;
- c*, cuticula;
- v*, vas deferens;
- d*, end of ductus ejaculatorius;
- ps*, penes or spicula;
- a*, anus.

presents a rounded terminus, which, inasmuch as the tail is destitute of glands (?), contains no aperture. The anus is not conspicuous and there is *no sign of a bursa*. The two equal, linear, acute, nearly straight spicula are wider and fusiform in the proximal third and are about twice as long as the tail or considerably longer than the anal diameter.* There are traces of accessory organs. The ductus ejaculatorius seems to be at least three to four times as long as the spicula. The testicle (or testicles; I do not know whether the male apparatus is single or double) appears to extend forward to near the median œsophageal bulb. The spermatozoa are large and spherical with conspicuous darker nuclei lying in the centre of the remaining translucent protoplasm. IV Fig. 6 represents a cross-section of the male taken from the region of the vas deferens, and shows the spermatozoa *in situ*, and also the size and relative position of the intestine. The left side of the figure is dorsal.

It only remains to say, concerning the structure of the male, that the tail, when seen in the dorsal or ventral aspect, presents a different contour from that shown when it is seen in profile, appearing in the former case to be somewhat concave-conoid.

From the foregoing description it will be seen that the males resulting from the moult in which the remarkable change of form occurs, are in all respects mature, being supplied with testicles and copulatory apparatus. With regard to the copulation I will venture to offer one or two suggestions. It is manifest that if the mature male had the form shown in Fig. 3, he would be much less perfectly adapted to making his way through the tissues of the root in which he has developed than if his form were a more slender one, and I can have no doubt that this fact explains the remarkable return to a slender form, shown in Fig. 6. The female, so far as I know (and I have examined quite a number, perhaps twenty), continues in the course already indicated—that is to say, never returns to a slender form, but, continuing the line of development shown in I, II, III, Fig. 1, becomes a motionless sac, whose sole object is the production of eggs. It would seem, then, that the copulation must take place inside the tissues of the plant infested, and that the males are enabled, by their return to the slender form, to make their way about in search of their obese and motionless female companions. The only other tenable hypothesis is that the males leave the plant, and that copulation occurs in the soil. This supposition has nothing in its favour which is not also in favour of the first supposition, and against it may be set up the two following suggestions:—(1) The female is not known to return to a slender form, and probably, after having once entered a root, never returns to the soil. (2) If the female does not return to the soil (and I must regard this as fairly well established by my observations) the only copulation that could occur in the soil would be between the males which had made their way outward and the females which had not yet entered. These females, however, do not, so far as I have observed, possess a vulva or any sexual apparatus beyond a rudiment consisting of a single cell, and are therefore incapable of copulating. What dim light my researches have shed on the subject compels me therefore to adopt the supposition that the males on assuming the slender adult form seek out and fertilize the females lying in the surrounding tissues. This supposition is possibly fortified by the absence of a bursa in the male, though I am not certain that the argument possesses much force. The fact is that the allied species (*Tylenchi*) possess a more or less complete bursa. There are reasons for regarding the bursa as a structure whose function is the attachment of the male to the female

* The reader will here trust the text and *not* the illustration. Fig. 6 (p 8) gives but a poor idea of the appearance of the spicula.

during copulation. If, however, the female were tightly held by the tissues of the root in which the copulation was to take place, it is easy to believe that a bursa would be of little service, and it might therefore disappear in the course of time because superfluous.

Fortunately I am better prepared to discuss the result of the fertilization. The ova in the uterus of the female, once they are fertilized, develop and surround themselves with a shell. The consequent increase in the size of the sexual organs causes them to fill a large proportion of the space contained in the sac-like body. Even when the worm has reached the proportions shown in II, Fig. 1, the ovaries and uteri occupy fully half the available space and the blind ends of the ovaries may often be seen projecting into the narrower part of the body. The remainder of the worm is filled with spherical clear spaces, the interstices among these spheres being filled up with granules. When the female has reached the mature stage represented in III, Fig. 1, the sexual apparatus occupies an even larger proportion of the body cavity.

The eggs have the form shown in Fig. 1, and have in many cases begun segmentation before they are deposited. The first two steps in the segmentation are shown in the figures. In accordance with the rule obtaining in the group Nematoda, the first two segments are unequal, though in the present case less unequal than usual. Of the first two segments, one begins to divide faster than the other, and gives rise to the exterior layer of a gastrula-like structure, while the other, dividing more slowly, gives rise to the internal cells of the same gastrula-like structure. The rapidity with which the segmentation goes on is in some degree indicated by the following experiment. On first receiving the Pretty Gully Scrub material, I placed some eggs in a moist chamber of peculiar construction. They were then in the first stages of segmentation. At the present time, three weeks later, they have reached the gastrula stage. It will therefore be seen that, provided the experiment be not deceptive, the embryonic life extends over a considerable period. The experiment needs, however, to be controlled by others before anything very positive can be said concerning the period of incubation. It is well known that the rapidity of segmentation in certain Nematodes varies widely according to the external conditions.

A word remains to be said with regard to the time and manner of depositing the eggs. Here again I must call attention to the incomplete state of my observations. So much is certain, that a relatively large vulva or sexual opening exists at the posterior extremity of the mature female. This appears as a flat conical projection, and is illustrated in the figures I and II, Fig. 1. In the neighbourhood of the vulva the surrounding root-tissue is usually of a yellow colour, and in this yellow tissue are uniformly to be found eggs, many of which are in the first stages of segmentation. I have also seen eggs well advanced which were still in the uterus. There seems, therefore, to be no great uniformity in the state in which the eggs are laid. But this important fact is established beyond doubt, namely, that the eggs are deposited in the root-tissues. Doubtless also they remain there until hatched. The larvæ must then either remove to fresh parts of the same root or, what is more probable, make their way into the soil in search of new rootlets. I assert the greater probability of the latter course for the following reasons:—The result of the attacks of the worms is abnormal tissue, and this is known sooner or later to decay. Therefore it follows that tissue already attacked is not an altogether suitable habitat. Moreover, old tissues are more or less impenetrable to the larvæ. They find their proper entrance only in the tender rootlets. Again, the larvæ are found in

abundance in the soil, showing that many must have left the tissues in which they were hatched. All this, however, does not preclude the supposition that some larvæ may simply move to a different part of the root in which they commenced their existence and there develop. I merely wish to point out that this is far less probable than that they attack fresh rootlets.

I have now related what I have learned concerning the life-history of this pest. Much remains to be done, and considering the extent of the devastation caused by allied worms in Europe and the United States, it is to be hoped that the remainder of the investigation will, in due time, be made. The importance of following the pest through the seasons of an entire year cannot be too strongly insisted upon. The manner in which this should be done is already indicated, and will now be still further elucidated. The exact time of year, if any exist, in which the larvæ issue in greatest numbers from old roots, and begin their migrations to fresh rootlets, should be ascertained. The manner in which the worms are spread from one field to another should be investigated. It is also important to ascertain whether or not the eggs or larvæ pass uninjured through the alimentary canal of domestic animals. If they are not injured by that process, manure is likely to become an agent in distributing the pest, for it is perfectly certain that root-crops injured by the worm will be fed to animals. Numerous researches, therefore, remain to be made before the pest can be said to have been properly investigated.

Systematic.

Although the foregoing observations are inadequate as a picture of the life history of this worm, they are quite sufficient to indicate its systematic position. Beyond doubt it must be referred to the genus *Tylenchus*, a genus already known to contain some of the worst enemies of various crops. *Tylenchus tritici* causing a serious disease in wheat, and *Tylenchus devastatrix*, which often sweeps off the onion crop in Europe, may be cited as instances. My reasons for assigning this worm a place in the genus *Tylenchus* must be given in full, for they affect also the systematic position of a number of worms heretofore reckoned as belonging to a distinct genus, *Heterodera*.

The characteristics of the genus *Tylenchus* may be briefly given as follows:—Transparent striated round worms, totally devoid of bristles or setæ, varying in length from one-third of a millimetre to three and a half millimetres, attacking the tissues of plants, or more rarely animals, by means of a spear and sucking apparatus of the following construction: A three-bulbed spear, capable of being thrust forth and withdrawn by means of appropriate muscles, is connected with a powerful median œsophageal sucking-bulb by means of a tube whose lining is more chitinous than is usual in other Nematode genera; the median bulb is connected with a smaller posterior bulb of much weaker construction by means of a shorter and weaker tube, which passes through the oblique nerve-ring, situated just behind the median bulb. The posterior bulb may become quite rudimentary, but probably never quite disappears. Lateral organs as well as visual organs are unknown in the genus. The female sexual apparatus is usually single and asymmetrical, being in that case usually straight and directed forward and often presenting a rudimentary posterior branch, but may be double and symmetrical. In the former case the vulva is behind the middle; in the latter case it is central. The male possesses two equal, arcuate spicula and a more or less well-developed bursa. From this characterization I have purposely omitted the changes that it will be necessary to make when the present worm and its allies are added to the genus.

It will be seen that the worm under consideration harmonizes with this characterization with slight exceptions. The male of the present worm has no bursa; but I cannot think this an objection to calling it *Tylenchus*. The bursa is very variable in *Tylenchus*, in some cases enveloping the tail completely, and in others extending only a short distance on either side of the anus, being in the latter case quite rudimentary. That it should fail completely cannot be regarded as even remarkable. Again the present worm presents a history, not hitherto admitted in the genus *Tylenchus*; but the remarkable change to the flask-like form is due merely to the degeneration of the digestive and muscular tissues on the one hand and an unusually luxuriant growth of the sexual organs on the other. The morphology of the animal is, it is true, thus obscured, but it is not materially changed. One never thinks of excluding certain species of *Rhabditis* from the genus to which they properly belong, merely because the young, as is often the case, finally rupture the uterus, and, entering the body cavity, devour its contents, and by growth finally give the body-wall of the mother-animal a bloated appearance. These two facts, the absence of the bursa, and the peculiar life-history consequent upon a truly parasitic life, are the main grounds for placing our worm in a genus separate from *Tylenchus*. Against these two objections, which are in reality slight, may be set up a vast array of arguments based on the similarity existing between it and *Tylenchus*. Let us consider in detail the exact proportions of a typical *Tylenchus*. For this purpose I have averaged the formulae of twenty species of this genus. The males of some of these species are as yet unknown, consequently I have first averaged the female formulæ, and with the following results:—

- (1.) Average female formula when the sexual organs are single, $\frac{1.9}{1.7} \frac{?}{?} \frac{18.1}{3} \frac{72.5}{3.4} \frac{88.9}{2.1} 1.23$.
- (2.) Average female formula when the sexual organs are double, $\frac{2.4}{?} \frac{?}{?} \frac{15.7}{?} \frac{50.0}{2.9} \frac{91.9}{?} 1.4$.

From the males which are known the following averages are obtained:—

- (3.) Average male formula when the female sexual organs are single, $\frac{1.9}{1.6} \frac{?}{?} \frac{19.6}{3} \frac{M}{3.2} \frac{88.1}{2.8} 1$.
- (4.) Average male formula when the female sexual organs are double, $\frac{2.8}{?} \frac{?}{?} \frac{18.2}{?} M \frac{95.5}{?} 1.29$.

Imperfect as these formulæ are, on account of our incomplete knowledge of many of the species, they serve to show at once the striking similarity existing between the worm we have under consideration and the typical *Tylenchus*. Compare the formula of the larva of the present species with the above formulæ, remembering always that the comparison is between a larva and adult forms, and that the relative length of the oesophagus and tail and all their component parts will in the larva decrease with age, as will also the relative width. It is evident at once that the resemblance is great in any case, and will ultimately be greatest between the worm whose affinity we are trying to discover and those *Tylenchi* whose females have double sexual organs. This is true, whether we compare the formula of our larva with the female formulæ of *Tylenchus* or compare the formula of our adult male with the male formulæ of *Tylenchus*. This result is all the more significant when we consider that the females of our species ultimately develop double sexual organs, and that species with blunt tails are relatively much more common in that group of *Tylenchi* whose females possess double sexual organs. There is not the slightest doubt left in my mind that we have here to do with a *Tylenchus* belonging to the group with double female sexual organs, which has, owing to a truly parasitic life, taken on some very striking but truly slight new morphological characteristics.

Before settling the specific relations of our worm, it will be necessary to review the literature of the subject. There can be no doubt that the worms heretofore described under the generic name *Heterodera* belong to the same generic group as that which we are considering. The resemblances to *H. Schachtii* (Schmidt) are too great to be overlooked for a moment. Our species, however, is not *Schachtii*. On comparison of the larvae and males of the two forms, it is at once evident that *Schachtii* is a wider worm, with a spear of different proportions, and with a longer oesophagus. Differences also exist in the formation of the mouth. The relations with *H. radicicola*, Greef and *H. Javanica* I cannot discuss, either on account of the incompleteness of the descriptions or the inaccessibility of the literature.

A work by Dr. J. C. Neal, on what is called the Root-knot Disease, has been recently issued by the Agricultural Department at Washington, U.S.A. The author describes a disease due to the attacks of a worm which he has provisionally named *Anguillula arenaria*. I have carefully examined the figures accompanying Dr. Neal's report and am convinced that the worm I have examined is identical with that which he has figured. His figures are such that the examination has not been easy. What I take to be the male of Dr. Neal's species, though he has called it a female (Plate XII, 6, Neal l. c. and XV, 1) gives the formulae $\frac{5.2}{2.4} \frac{8.7}{2.8} \frac{13.0}{3.2} M \frac{?}{7.1} \frac{1.5}{4.5} \frac{23.3}{4.6} M \frac{?}{5.4} \frac{?}{2.7}$. His larvae give $\frac{1.4}{1.7} \frac{?}{4.6} \frac{12.2}{5.4} M \frac{?}{6.4} \frac{?}{2.7}$. The great width of these figures I can attribute to pressure from the cover-slip. Otherwise there is a fair amount of correspondence between his figures and my own. It is, however, best to mention the following points. *A. arenaria*, Neal, is said to be indigenous in the United States. Its uteri often contain living and hatched embryos. The eggs are said to escape by rupture at the anterior end. I think this is a mistake, and that Dr. Neal has shown the vulva in Plate XIX near the lower margin of his figure, and again more plainly in Plate XXI. Dr. Neal does not figure a bulb in all cases, but it may easily have been overlooked. As I have already stated, much of the work in the investigation of free-living Nematodes lies on the very verge of what can be accomplished with the best modern microscope. In no part of the paper is the spear mentioned as such, but I cannot help regarding the words "fissure having a circular hinge-like termination," as the author's interpretation of the Tylenchoid spear. Still I call attention to the fact that if I am right in this, Dr. Neal's figures represent the spear as much larger than I have found it to be. The eggs are figured in the American pamphlet as straight. I have observed that they are usually slightly curved. In spite, however, of these minor differences, which are, for the most part, I think, to be attributed to the American investigator's acknowledged unfamiliarity with Nematode anatomy, I can have no doubt that the Australian worm is the same that Dr. Neal has described as occurring in a belt of land one hundred and fifty miles wide extending from Texas through the Gulf and South Atlantic States, a distance of, say, two thousand miles. This being the case, I shall for the present call the Australian worm, *Tylenchus arenarius*, Neal, with the remark that for aught I can say to the contrary, it may be *T. (Heterodera) radicicola*, Greef, or *T. (Heterodera) Javanicus*.

Dr. Bancroft, of Brisbane, has sent me an interesting pamphlet in which he describes and figures a root-infesting Nematode found by him on grape and banana roots. Dr. Bancroft's well-known familiarity with Nematode anatomy has enabled him to distinguish both sexes. His figures seem to represent *T. arenarius*.

II.

THE GENUS TYLENCHUS.

(Character given on page 164.)

KEY WHEN BOTH SEXES ARE KNOWN.

<i>Female sexual apparatus, double</i> :—			Page.
Species leading a parasitic life in roots of various plants—			
<i>(Esophagus of the larva 26; width 6)</i>	2	<i>Schachtii</i>	170
<i>(Esophagus of the larva 18; width 3·6)</i>	3	<i>arenarius</i>	170
<i>(Insufficiently known to me at this point are T. radicicola and T. Javanicus.)</i>			
Species leading a free existence—			
Tail of female rounded at the end—			
Length of female 1·7 mm.; width 2·5	4	<i>robustus</i>	170
Length of female 1·5 mm.; width 4'	5	<i>dubius</i>	171
Tail of female conical—			
Cuticula with no very conspicuous wings; spear stout	6	<i>gracilis</i>	171
Cuticula with two lateral and four submedian wings; spear slender	7	<i>lamelliferus</i>	171
<i>Female sexual apparatus, simple (single), often with a rudimentary posterior branch</i> :—			
<i>(Esophagus Tylenchoid, i.e., with one or more bulbs; parasitic in bees)</i>	1	<i>bombi</i>	169
<i>(Esophagus Tylenchoid; if parasitic then in plants)</i>			
Bursa of male completely enveloping the tail—			
Tail of female rounded at the end—			
Vulva 75' +; tail conoid	8	<i>pratensis</i>	171
Vulva 67'; tail nearly cylindroid	9	<i>obtusus</i>	172
Tail of female conical—			
Length 1·5 mm.,	10	<i>terricola</i>	172
Length 1· mm. or more—			
Spicula L-shaped	11	<i>imperfectus</i>	172
Spicula straight or arcuate—			
Accessory pieces as long as the spicula ..	12	<i>fungorum</i>	172
Accessory pieces shorter than the spicula—			
<i>(Esophagus (female) 4·2)</i>	13	<i>scandens</i>	173
<i>(Esophagus (female) 16·7)</i>	14	<i>devastatrix</i>	173
Bursa of male incompletely enveloping the tail—			
Length of the cesophagus indefinite; tail 95'	15	<i>velatus</i>	174
Length of the cesophagus definite—			
Anus 67' to 70'—			
Vulva central; width 2'	16	<i>leptosoma</i>	174
Vulva 60'; width 3·5	17	<i>filiformis</i>	174
Anus 84' or more—			
Neck 27' to 29'—			
Vulva 83'; spear 5·5.	18	<i>macrophallus</i>	174
Vulva 70'; spear 2'....	19	<i>pilludifer</i>	174
Neck 15 to 20'—			
Spear stout; conspicuously bulbed.....	20	<i>Davainii</i>	175
Spear weak; inconspicuously bulbed—			
Width 2·9; bursa extending to middle of tail ..	21	<i>intermedius</i>	175
Width 2·1; bursa shorter	22	<i>elegans</i>	175
<i>(Esophagus Dorylaimoid, i.e. lachrymatoriform)</i>	23	<i>Askanaseyi</i>	176
	24	<i>mirabilis</i>	176

NOTES ON THE KEY.

- The keys assume the unknown male of *terricola* to have a bursa completely enveloping the tail.
- The figures throughout refer to percentage of the length of the worm unless otherwise stated.

In case only one sex is known the following keys will be found useful:—

KEY TO MALES.

Bursa none—			Page.
Spear 1°; œsophagus 13°	3	<i>arenarius</i>	170
Spear 4°; œsophagus 7°	2	<i>Schachetii</i>	170
Bursa completely enveloping the tail—			
Œsophagus 23° to 24°—			
Length '77 mm.; width 4·3.....	9	<i>obtusus</i>	172
Length '45 mm.; width 3·7.....	8	<i>pratensis</i>	171
Œsophagus 18° or less—			
Spear a mere point or invisible—			
Spicula L-shaped.....	11	<i>imperfectus</i>	172
Spicula straight	12	<i>fungorum</i>	172
Spear distinct—			
Length at least 2 mm.—			
Width 3·5.....	13	<i>scandens</i>	173
Width 1·4.....	6	<i>gracilis</i>	171
Length 1·5 mm. or less—			
Width about 4°—			
Cuticula with two lateral and four submedian wings	7	<i>lamelliferus</i>	171
Cuticula with no such conspicuous wings	5	<i>dubius</i>	171
Width 3° or less—			
Anus 97·5; spear 4°	4	<i>robustus</i>	170
Anus 93·5; spear 1°	14	<i>devastatrix</i>	173
Bursa incompletely enveloping the tail—			
Anus about 67°—			
Width 3·3.....	17	<i>filiformis</i>	174
Width 1·9.....	16	<i>leptosoma</i>	174
Anus 85° or more—			
Œsophagus indefinite with no bulbs	15	<i>velatus</i>	174
Œsophagus definite—			
Neck 27° to 29°—			
Spear large (5·5); spicula long	18	<i>macrophallus</i>	174
Spear shorter (2°)	19	<i>pillulifer</i>	174
Neck 20° or less—			
Width 5°; œsophagus 10°	23	<i>Askanaseyi</i>	176
Width 3·6 or less; œsophagus 15° or more—			
Spear stout; conspicuously bulbed	20	<i>Davainii</i>	175
Spear weak; inconspicuously bulbed—			
Œsophagus 15°; tail 85°	22	<i>elegans</i>	175
Œsophagus 20°; tail 90°	21	<i>intermedius</i>	175

KEY TO FEMALES.

Female sexual apparatus double :—

Page.

Tail and anus none ; saccate worms parasitic in roots—			
Body widely fusiform	2	<i>Schachtii</i>	170
Body ellipsoidal or spherical	3	<i>arenarius</i>	170
Tail rounded at the terminus—			
Length .75 mm. ; œsophagus 18	5	<i>dubius</i>	171
Length 1.70 mm. ; œsophagus 12.5	4	<i>robustus</i>	170
Tail conical—			
Cuticula with two lateral and four submedian wings ...	7	<i>lamelliferus</i>	171
Cuticula with no such conspicuous wings	6	<i>gracilis</i>	171

Female sexual apparatus simple (single) :—

Œsophagus Tylenchoid, i.e., with one or more bulbs ;			
parasitic in bees	1	<i>bombi</i>	169
Œsophagus Tylenchoid ; if parasitic then in plants—			
Tail conoid terminus not rounded—			
Neck only 4.2	13	<i>scandens</i>	173
Neck 10.—			
Vulva 92'	12	<i>fungorum</i>	172
Vulva 80'	23	<i>Askanaseyi</i>	176
Neck 14 to 19.—			
Vulva central	16	<i>leptosoma</i>	174
Vulva about 67.—			
Anus 70'	17	<i>filiformis</i>	174
Anus 85' or more—			
Length .54 mm ; width 4'	10	<i>terricola</i>	172
Length .85 mm, to 1 mm.—			
Width 2.1	21	<i>intermedius</i>	175
Width about 3.—			
Spear 1.2, hardly knobbed	22	<i>elegans</i>	175
Spear 1.9, distinctly 3-knobbed	20	<i>Davainii</i>	175
Vulva 80 or more—			
Œsophagus 14' ; vulva 88'	11	<i>imperfectus</i>	172
Œsophagus 16.7' ; vulva 80'	14	<i>devastatrix</i>	173
Neck 27 to 29.—			
Anus 92' ; vulva 83'	18	<i>macrophallus</i>	174
Anus 85' ; vulva 70'	19	<i>pillulifer</i>	174
Tail rounded at the terminus—			
Vulva 75'+ ; tail conoid	8	<i>pratinensis</i>	171
Vulva 67' ; tail nearly cylindrical	9	<i>obtusus</i>	172
Œsophagus Dorylaimoid, i.e. lachrymatoriform	24	<i>mirabilis</i>	176

1. *T. bombi*, Dufour. The young of this remarkable species are worms about one millimetre long, living free in the soil, where they become mature and copulate. The fertilized females enter the bodies of hibernating bees, and there lead a parasitic existence, occupying either the body cavity or the wall of the alimentary canal. During the parasitic life the sexual apparatus protrudes from the vulva, and ultimately becomes a sac one and a half millimetres long, to which is attached for some time the real body of the worm in the form of a small appendage; but even this finally disappears. In this latter condition the animal first became known under the name of *Sphaerularia bombi*. The young, to the number of 50,000 to 100,000, hatch while still in the body of the host, but become sexually perfect only on entering the soil.

2. T. Schachtii, Schmidt. $\frac{7.4}{5} \frac{22.6}{6.4} \frac{26.1}{5.8} M. \frac{86.6}{3.6}$: 36 mm. is the formula* for the freshly hatched larvæ, of which the following is a further description:— Neck cylindroid to opposite the base of the spear, thence convex-conoid to the rather narrow but unusually prominent and projecting lip region; spear bulbous at its base; anterior part of the œsophagus a narrow chitinous canal, which leads to a muscular prolate bulb two-thirds as wide as the adjacent part of the neck; nerve-ring close behind the bulb just mentioned; remainder of the œsophagus apparently indistinct, certainly short; intestine three-fourths as wide as the body, terminating posteriorly in a rectum one-third as long as the anal diameter; tail conical; rudimentary sexual apparatus a little in front of the commencement of the posterior third of the body.

The larvæ, which are found in the soil, make their way into rootlets of various plants by means of the special piercing and sucking apparatus (spear and bulb), and then undergo a remarkable metamorphosis, similar to that already described in the case of *T. arenarius*, Neal. At an early moult they lose the conical tail, a shorter and rounded one taking its place. Meanwhile the body, amply nourished by plant juices, becomes plump, and takes on the dimensions shown in the following formula:— $\frac{4.9}{7.4} \frac{20.7}{3.4} \frac{?}{?} M. \frac{98.5}{15.7} \frac{?}{6.4}$.

The sexual organs now begin to develop, and the larva become elongated sac-shaped. The female continues to develop in this manner, and becomes finally a motionless, widely fusiform sac, devoid of anus and with a terminal vulva. The two-parted female sexual apparatus develops enormously, and at last fills the body of the worm completely. The number of eggs contained in it averages 300 to 400. These are deposited in the tissue of the plant attacked at a period when they contain well-developed embryos. The male, however, instead of continuing in the path of development followed by the female, returns to a slender form, having the following dimensions:— $\frac{4.3}{3} \frac{15.5}{3} \frac{17.}{3} M. \frac{97.4}{3}$. The structure of the head and œsophagus is quite similar to that of the newly-hatched larvæ. The tail, however, becomes nearly hemispherical. The linear-cuneiform spicula are arcuate and acute. There is no bursa and the testicle extends to the middle of the body at least. The change of the male to the slender form occupies at least five or six days. Nothing is known concerning the copulation. The eggs laid by the female are .04 x .08 mm. The males and females are born in equal numbers, and the change from the egg to the adult state occupies from five to six weeks.

This worm is the cause of a most serious disease in the sugar-beet. For remedies, see those recommended for *T. arenarius*.

3. T. arenarius, Neal. Sufficiently described in the foregoing pages. For remedies, see section III.

4. T. robustus, De Man. $\frac{2.4}{?} \frac{?}{?} \frac{12.5}{?} \frac{50+}{2.5} \frac{98.2}{?} 1.7$ mm. Cuticula finely striated; heterocephalous, lipless; two lateral and four submedian chitinous edges (soon disappearing) found on the head; spear very stout; median bulb ovoid; *porus excretorius*, at ten per cent.

$\frac{4.1}{?} \frac{?}{?} \frac{18.3}{?} M. \frac{97.5}{2.9} 1.3$ mm. Neck, as in the female, diminishing considerably; tail completely enveloped by the bursa, which presents two lateral papillæ on the post-anal part; the short spicula accompanied by rod-shaped accessory pieces.

This slow moving species is rather common in Holland, in soil penetrated by fresh or brackish water.

* For an explanation of the formulae used in this report see the first number of this *Gazette*, p. 131.

5. **T. dubius**, Bütschli. $\frac{3}{2.9} \frac{8.21}{3.6} \frac{18.}{4.} \frac{50.4}{4.} \frac{92.3}{?} .75$ mm. Cuticula presenting about seven hundred fifty transverse striae. The rounded head is destitute of papillæ and lipless, although a lip region is set off by constriction; prolate median bulb central, one-half as long as the adjacent part of the neck is wide; conoid posterior swelling nearly as wide as the intestine, which is two-thirds as wide as the body and composed of cells loosely packed with granules; *porus excretorius* at twelve per cent.; tail cylindroid, diminishing at last.

$\frac{3}{2.9} \frac{8.21}{3.6} \frac{18.}{4.} \frac{M}{4.} \frac{93.4}{2.8} .75$ mm. Tail, unlike that of the female, conical and completely enveloped by the bursa, which extends far enough forward to be symmetrically arranged with respect to the anus, and presents at the middle of the tail a pair of ribs extending nearly to the margin; a single indistinct median papilla opposite the proxima of the linear spicula; these latter nearly two-thirds as long as the tail, arcuate in the distal two-thirds, and presenting proximæ cephaloid by a broad constriction; accessory pieces one-half to two-thirds as long as the spicula.

This species has been found on roots of plants at Frankfort-on-the-Main and also Jena, Germany, and in Holland.

6. **T. gracilis**, De Man. $\frac{1.}{?} \frac{?}{?} \frac{?}{?} \frac{50.4}{14} \frac{94.4}{?} 22+mm.$ Striae of the cuticula exceedingly fine; neck diminishing but little; slightly heterocephalous, the head being short and rounded in front; spear stout and furnished with three large bulbs at the base; posterior margin of the median bulb at five per cent.; posterior end of the oesophagus not distinctly seen; *porus excretorius* opposite the posterior margin of the median bulb; lateral markings on the head.

$\frac{1.}{?} \frac{?}{?} \frac{?}{?} \frac{M}{1.4} \frac{95.}{?} 21$ mm. Bursa completely enveloping the conical posterior extremity, and presenting lateral papillæ a little behind the middle of the tail; the small plump spicula accompanied by short somewhat arcuate accessory pieces.

Rare in forest and meadow ground, Holland.

7. **T. lamelliferus**, De Man. $\frac{2.8}{?} \frac{?}{?} \frac{16.7}{?} \frac{50.4}{3.9} \frac{94.8}{?} 1.$ mm. Cuticula with exceedingly fine striae; two lateral and four submedian wings throughout the length; neck diminishing somewhat to the homocephalous, rounded anterior extremity; lips and papillæ none; spear long but slender, with distinct bulbs at the base; median oesophageal bulb large; *porus excretorius* situated between the median bulb and the intestine; terminus of the tail rounded.

$\frac{3}{?} \frac{?}{?} \frac{18.2}{?} \frac{M}{3.9} \frac{96.2}{?} 1.$ mm. Bursa completely enveloping the posterior extremity, somewhat peculiarly narrowed in front of its posterior terminus, and presenting two lateral papillæ a little in front of the middle of the tail; the stout spicula accompanied by rod-like arcuate accessory pieces.

Rather common in moist ground, Holland.

8. **T. pratensis**, De Man. $\frac{2.7}{?} \frac{?}{?} \frac{24.}{?} \frac{75.4}{3.7} \frac{96.}{?} .66$ mm. Neck diminishing but little to the somewhat heterocephalous discoid anterior extremity, which presents two lateral chitinous markings; lips and papillæ none, spear very stout; median bulb nearly spherical, the posterior swelling pocket-shaped; *porus excretorius* at sixteen per cent.; lateral fields one-fourth as wide of the body.

$\frac{2.7}{?} \frac{?}{?} \frac{21}{?} \frac{M}{\frac{9.6}{?}} \frac{9.6}{?}$.45 (- .6 ?) mm. Two papillæ near the end of the bursa; the slightly arcuate spicula, accompanied by short arcuate accessory pieces. A slow-moving species found in meadows and marshy ground in Holland.

9. *T. obtusus*, Bastian. $\frac{2.5}{?} \frac{?}{?} \frac{23.5}{4} \frac{M}{\frac{9.3}{3}} \frac{9.3}{?}$.48 mm. Cuticula presenting about seven hundred transverse striae; conoid neck terminating in a truncate head; lips and papillæ none; spear stout and bulbed; ellipsoidal median bulb situated at ten per cent., one-half as wide as the adjacent part of the neck; cardiac collar distinct; the granular intestine terminating posteriorly in a rectum whose length is equal to that of the anal diameter; *porus excretorius* at fourteen per cent.

$\frac{2.5}{3} \frac{?}{?} \frac{23.5}{4} \frac{M}{\frac{9.3}{3}} \frac{9.3}{?}$.77 mm. Tail convex conoid; bursa beginning opposite the proximæ of the oblong, somewhat arcuate spicula, which are as long as the anal diameter and accompanied by accessory pieces half as long.*

Rootlets of oats, England.

10. *T. terricola*, Bastian. $\frac{2.2}{?} \frac{?}{?} \frac{16.7}{4} \frac{6.7}{4} \frac{9.9}{1.6}$.54 mm. Conoid neck terminating in a truncate head; ellipsoidal median bulb situated at about ten per cent.; posterior swelling none (?); *porus excretorius* at twelve per cent. Male unknown.

Rootlets of wheat, England.

11. *T. imperfectus*, Bütschli. $\frac{1.4}{1.6} \frac{?}{?} \frac{13.9}{?} \frac{-M^{7.8}}{3} \frac{9.2}{1.6}$.88^{7.4} mm. Spear bulbed; lateral fields finely granular; tail conical from the vulva; uterus short, mostly with one egg, and that segmenting; oviparous; mature when only eight-tenths of a millimetre long.

$\frac{1.4}{1.6} \frac{?}{?} \frac{13.9}{?} \frac{-M^{7.8}}{3} \frac{9.2}{1.6}$ Considerably smaller than the female; spear a mere point; tail concave-conoid, the large and wide bursa extending even a little beyond the end of the tail and far enough forward to be symmetrically arranged with respect to the anus; ribs none (?); spicula twice as long as the anal diameter and bent in the middle, the proximal halves being twice as wide as the distal halves; proximæ cephaloid by a broad constriction; accessory pieces none.

Decaying fungi, Frankfort-on-the-Main, Germany. Related to number 12.

12. *T. fungorum*, Bütschli. $\frac{5(?)}{1.4(?)} \frac{6.5}{2.2} \frac{10.4}{2.7(1.6)} \frac{22^{81}}{3.2} \frac{8.5}{1.6}$.3 mm. Cuticula presenting about fifteen hundred transverse striae; conoid neck terminating in a truncated head, which is probably lipless and devoid of papillæ; oesophagus indistinct and without bulbs (?); cells of the intestine with a few large granules; rectum nearly equalling the anal diameter in length; lateral fields two-fifths as wide as the body, the dorsal field narrow; uterus nearly half as long as the body and containing many spherical or ellipsoidal unsegmented eggs each two-thirds as long as the body is wide.

$\frac{?}{?} \frac{?}{?} \frac{?}{?} \frac{M}{?} \frac{9.4}{?}$ 1.6 mm. Tail conical, hooked in the larvæ; more than half of the bursa in front of the anus; a double ventral post-anal papilla opposite the middle of the accessory pieces, and a single one opposite their ends; the straight spicula somewhat dumb-bell shaped, and a little longer than the anal diameter; the forked accessory pieces as long as the spicula, extending backwards and terminating in extremities turned ventralwards.

Found in decaying fungi, Frankfort-on-the-Main, Germany.

* Bastian's text and figures disagree with regard to the length of the oesophagus of this species.

13. *T. scandens*, Schneider. $\frac{1}{7} - \frac{2}{3} - \frac{4.2}{1.6} - \frac{89.7}{3} - \frac{97.2}{1}$ 3-63 mm. Somewhat spirally curved; cuticula with two thousand five hundred striae; spear with three bulbs at the base; median bulb at one and eight-tenths per cent.; *porus excretorius* at three and one-tenth per cent.; lateral fields one thirtieth as wide as the body.

$\frac{2}{7} - \frac{2}{7} - \frac{2}{7} - M - \frac{90.1}{3.5} - \frac{17-2.3}{1}$ mm. Straight; spicula one-third as wide as long, shorter than the anal diameter; the accessory pieces one-third as long and much more slender. (Syn., *T. tritici*, Bast., *Anguillula tritici*, Needh.)

The young or larvæ, to the number of eight or ten, are found in so-called "gouty" wheat-grains. The portion of the grain usually occupied by the embryo becomes in consequence powdery and incapable of germinating. When the wheat is sown the larvæ bore their way through the weakened wall of the diseased grain and pass out into the soil, where they attack and enter sprouting wheat grains. Here they remain for a time—perhaps the whole winter through—without change. When the wheat starts on its spring growth the larvæ make their way into the flower-bud, become mature, copulate, and after producing a new clutch of eggs, die. The eggs hatch, and the resulting larvæ penetrate the new wheat-grains, and soon become their only contents, the above-mentioned powder excepted. If infested wheat be stored, even for many years, the larvæ still remain alive, ready to make their way out of the grains whenever the wheat is sown. The disease occurs in many parts of Europe.

Remedy.—Inspect the grain, and reject all "gouty" seed-wheat.

14. *T. devastatrix*, Kühn. $\frac{1}{1} - \frac{2}{2} - \frac{16.7}{2.3} - \frac{80}{2.5} - \frac{93.5}{2.2} - 1 - 1.5$ mm. Marked with about two hundred twenty transverse striae; the conoid neck terminates in a truncate head devoid of lips and papillæ; spear-bulbed at the base; cesophagus one-sixth as wide as the neck; median bulb small, the posterior large; *porus excretorius* lying near the median bulb; intestine terminating in a rectum two-thirds as long as the anal diameter; tail diminishing from the vulva, convex-conoid behind the anus; vulva prominent; rudimentary posterior branch of the sexual apparatus sac-like and extending half way to the anus; eggs twice as long as wide; viviparous or ovi-viviparous.

$\frac{1}{1} - \frac{2}{2} - \frac{16.7}{2.3} - M - \frac{93.5}{2.2} - 1 - 1.5$ mm. Tail conoid, diminishing more rapidly near the anus, sometimes constricted behind the middle, as is also that of the female; bursa commonly springing from near the anus, devoid of ribs, somewhat variable; spicula cuneiform, slightly arcuate, less than half as long as the anal diameter; arcuate accessory pieces one-third as long as the spicula. (Syn., *T. allii*, Beyerinck; *T. dipsaci*, Kühn; *T. Hyacinthi*, Prilleux; *T. Haversteinii*, Kühn.)

Found in many parts of Europe. There is reason to believe that it exists also in Australia. A most destructive parasite, attacking many varieties of cultivated plants. It sometimes sweeps off the onion crop in Belgium. It attacks teasel, hyacinths, rye, oats, buck-wheat, potatoes, &c. It commonly prefers the flower and fruit, but may attack any part of the plant. In rye it causes "knots" or galls; in potatoes it causes a disease similar in appearance to the potato-rot due to *Peronospora infestans*.

Remedy.—Difficult to deal with. Can be starved out by keeping the land free of vegetation of every description. It may probably be trapped like *T. Schachtii*, though I do not know of any cases in which it has been

dono. This worm is said to be killed by the digestion of domestic animals, so that manure could not be infected except by bits of bedding, &c., used in stalls. This worm is not injured by moderate desiccation.

15. *T. velatus*, Bütschli. Female unknown. $\frac{1.3}{1} - \frac{?}{?} - \frac{M}{2.6} - \frac{63}{1.8} - \frac{55}{1.8}$ mm. The conical neck terminating in a head devoid of lips and papillæ and appearing emarginate in optical section; spear rather slender, bulbed at the base; œsophagus seemingly devoid of bulbs; *porus excretorins* at fourteen per cent.; tail conical, almost completely enveloped by a bursa devoid of ribs; spicula cuneiform, equalling the anal diameter in length; accessory pieces (?).

Roots of moss, Frankfort-on-the-Main, Germany.

16. *T. leptosoma*, De Man. $\frac{1.6}{?} - \frac{?}{?} - \frac{18.8}{?} - \frac{55}{1.9} - \frac{66.7}{?}$ mm. Striae exceedingly fine; neck tapering much; homocephalous, the head rounded in front; lips and papillæ none; spear weak, bulbed; œsophagus distinct; median bulb ellipsoidal; tail conical, the terminus setaceous.

$\frac{1.6}{?} - \frac{?}{?} - \frac{18.8}{?} - \frac{M}{1.9} - \frac{66.7}{?}$ mm. Tail like that of the female; bursa extending but a short distance on each side of the anus; spicula slender and devoid of accessory pieces.

Very common in moist soil, Holland.

17. *T. filiformis*, Bütschli. $\frac{2.3}{?} - \frac{?}{?} - \frac{18.8}{?} - \frac{60.40}{3.2} - \frac{70.4}{2.4} - \frac{55}{1.8}$ mm. Two hundred and fifty striae; heterocephalous, the head being rather long, rounded in front, and devoid of lips and papillæ; spear bulbed; median œsophageal bulb ellipsoidal, situated at one-third the distance from the mouth to the intestine; cardiac bulb larger, and of about the same shape; cardiac collar broad and indistinct; cells of the intestine coarsely granular; rectum longer than the anal diameter; *porus excretorins* at twelve per cent.; lateral wings distinct; vulva inconspicuous; rudimentary posterior branch of the sexual organs reaching one-fourth the distance to the anus; eggs as long as the body is wide and one-half as wide as long.

$\frac{2.3}{2} - \frac{?}{?} - \frac{18.3}{3.1} - \frac{M}{3.3} - \frac{68}{2.4} - \frac{55}{1.8}$ mm. Tail like that of the female; bursa like that of number 16; spicula slender, arcuate, and unaccompanied by accessory pieces.

Frankfort-on-the-Main, Germany, and in Holland; common in the soil.

18. *T. macrophallus*, De Man. $\frac{6.9}{?} - \frac{?}{?} - \frac{27.6}{?} - \frac{83}{4.2} - \frac{92.4}{?} - \frac{57}{1.8}$ mm. Cuticular finely striated; neck tapering but little; homocephalous, the head being truncate in front and devoid of lips and papillæ; spear large and stout; median bulb larger in the female than in the male; posterior end of the œsophagus widened and pocket-shaped; *porus excretorins* at twenty per cent.; tail conical.

$\frac{5.5}{?} - \frac{?}{?} - \frac{27.6}{?} - \frac{M}{3.6} - \frac{90.9}{?} - \frac{53}{1.8}$ mm. Tail conical; bursa like that of the two preceding species; spicula large, somewhat arcuate, acute, unusually long, with short, rod-like arcuate accessory pieces.

An active species, rare in fresh-water meadows, Holland.

19. *T. pillulifer*, Von Linstow. $\frac{2}{1.4} - \frac{?}{?} - \frac{29.2}{2.2} - \frac{70}{2.6} - \frac{81.5}{?} - \frac{54}{1.8}$ mm. Neck conoid to the rather rounded head, which appears in optical section to be deeply emarginate; spear bulbed; œsophagus cylindroid, over one-third as wide as the neck; *porus excretorins* at twenty per cent.; tail conical.

$\frac{2}{1.4} \frac{?}{?} \frac{29.2}{2.2} \frac{M}{2.6} \frac{61.5}{2.1} \cdot 38$ mm. Tail conical; bursa nearly symmetrical with respect to the anus, ending posteriorly near the middle of the tail; spicula one-fourth as long as the tail.

Water, Ratzeburg, Germany.

20. **T. Davainii**, Bastian. $\frac{1.9}{1.7} \frac{?}{?} \frac{11.2(?)}{2.8} \frac{54}{3.1} \frac{67.37}{3.2} \frac{86}{2.1} \cdot 1$ mm. About six hundred transverse striae, hardly heterocephalous, the head being concave-truncate in front; almost lipless, papillæ none; spear 3-bulbed at the base; ellipsoidal median bulb one-half to two-thirds as wide as the neck; posterior end of the œsophagus widened in front of the distinct cardiac collar; intestine one-half as wide as the body, the contents of its cells granular; rectum as long as the anal diameter; *porus excretorius* at twelve per cent.; lateral fields rather broad; nerve-ring oblique; tail conoid from the inconspicuous anus and possessing caudal glands; terminus conical, narrow; vulva inconspicuous; rudimentary posterior branch of the sexual apparatus one-half as long as the adjacent portion of the body is wide; eggs twice as long as the body is wide, and less than one-third as wide as long.

$\frac{1.9}{1.7} \frac{?}{?} \frac{18.7}{3.3} \frac{-M}{3.6} \frac{54}{2.6} \frac{65.2}{2.6} \cdot 1$ mm. Tail like that of the female; bursa symmetrically arranged with respect to the anus, appearing when seen in profile to be twice as long as the spicula; spicula somewhat irregularly arcuate-cunciform, as long as the anal diameter, and accompanied by slender accessory pieces half as long.

England, Germany, Holland, and Australia. Very common, being the typical species of the genus. I have observed the position of the nerve-ring in a single Australian specimen, and therefore permit its position to stand as questionable for the present.

21. **T. intermedius**, De Man. $\frac{?}{?} \frac{?}{?} \frac{16.7}{?} \frac{67.1}{2.1} \frac{86.7}{?} \cdot 85$ mm. Cuticula very finely striated; neck diminishing considerably to the somewhat heterocephalous anterior extremity, which has a hemispherical form and is destitute of appendages; œsophagus distinct, widening to form a very small ellipsoidal median, and a pocket-shaped posterior bulb; *porus excretorius* at eleven per cent.

$\frac{1}{?} \frac{?}{?} \frac{29}{2.1} \frac{M}{?} \frac{90.3}{?} \cdot 85$ mm. Tail conical; bursa springing from a little in front of the anus; ribs and papillæ none; spicula rather plump, accompanied by weak, linear, areuate accessory pieces one-third as long.

An active species, found in fresh and brackish soil, Holland.

22. **T. elegans**, De Man. $\frac{1.2}{?} \frac{?}{?} \frac{15}{?} \frac{67}{2.9} \frac{85}{?} \cdot 1$ mm. Striae of the cuticula exceedingly fine; neck diminishing considerably to the barely heterocephalous hemispherical anterior extremity; lips and papillæ none; œsophagus with a rather small median bulb and a posterior widening; *porus excretorius* variable; tail conical.

$\frac{1.2}{?} \frac{?}{?} \frac{15}{?} \frac{M}{2.9} \frac{85}{?} \cdot 1$ mm. Tail conical; bursa small, symmetrically arranged with respect to the anus; spicula slightly arcuate, with slightly arcuate accessory pieces one-third as long. (Syn. *T. exiguum*, De Man.)

Moist soil, Holland. Becomes sexually perfect when small.

23. T. Askanaseyi, Bütschli. $\frac{8}{1\cdot2} \frac{?}{?} \frac{10^{\circ}}{2\cdot8} \frac{80^{\circ}}{(5\cdot2)} \frac{91\cdot3}{3\cdot3} \frac{1\cdot7}{1\cdot3}$ mm. Cuticula smooth (?); the fusiform body continued in front by a convex-conoid neck; lip region distinct; spear with a three-bulbed base; oesophagus one-eighth to one-fifth as wide as the neck, expanding to form a median bulb twice as wide; posterior bulb one-fourth as long as the oesophagus and half as wide as the adjacent part of the neck, and containing a cell; cardiac collum not very distinct; cells of the yellowish-brown intestine filled with granules; rectum twice as long as the anal diameter; wings present; tail conoid, its terminus pointed; vulva prominent; rudimentary posterior branch of the sexual apparatus extending more than half-way to the anus; the unsegmented eggs as long as the body is wide and half as wide as long.

$\frac{8}{1\cdot2} \frac{?}{?} \frac{10^{\circ}}{2\cdot8} \frac{-M}{3^{\circ}} \frac{91\cdot7}{2\cdot2} \frac{1\cdot1}{1\cdot1}$ mm. Tail conoid from the inconspicuous anus; bursa springing from opposite the proximæ and extending to the middle of the tail; spicula cuneiform, slightly arcuate, one and one-half times as long as the anal diameter and accompanied by linear accessory pieces one-third as long.

Males and females equally abundant among the leaves of moss; Germany.

One to two dozen adult worms are found among the leaves of a moss-bud, accompanied by countless young. The latter develop in the moss-bud until as large as the parent worms ($1\cdot x 0\cdot028$ mm), the sexual organs, however, remaining very rudimentary. Sexual maturity seems to be reached only after a residence in the soil, and when the young worms have made their way into the buds of young moss-plants, and is then, as in *T. fungorum*, probably attained at a single moult.

24. T. mirabilis, Bütschli. $\frac{3\cdot2}{2\cdot4} - \frac{?}{?} \frac{27\cdot5}{4^{\circ}} \frac{6\cdot8^{18}}{4^{\circ}} \frac{96}{3\cdot2} \frac{1\cdot1}{1\cdot1}$ mm. Cuticula striated; neck convex-conoid; heterocephalous, the head being about hemispherical; lips and papillæ indistinct; spear slender, bulbed, hollow; oesophagus in its anterior part one-third as wide as the neck, a little behind the middle becoming rather suddenly twice as wide; cardiac collum not deep but distinct; rectum one-third as long as the anal diameter; tail convex-conoid to the rounded terminus; vagina two-thirds as long as the body is wide, thick-walled; ovary reflexed to near the vulva; male unknown.

Only one specimen has been seen. Roots of moss, forest, Frankfort-on-the-Main, Germany.

NOTE.—It is in order to place in the annals of Australian literature a connected account of the important genus *Tylenchus* that I have inserted the foregoing summary, in which I include the species hitherto referred to the genus *Heterodera*, inasmuch as I believe them to be in reality species differing in no very essential manner from those constituting the group *Tylenchus*. I venture to hope that with the aid thus afforded any one familiar with the use of the microscope will be able to recognize the different species of *Tylenchus*. Where there are so many capable microscopists it is reasonable to hope that some will now and then turn their attention to the exceedingly interesting and important group of animals of which *Tylenchus* is a member. It will be necessary to spend a few moments in mastering the formula used. For this purpose the reader is referred to page 131 of the first number of this *Gazette*. For the convenience of those most familiar with the English unit of microscopic measurement it is deemed best to insert here the following

Rule.—To convert millimetres into inches, or thousandths of a millimetre (μ) into thousandths of an inch, multiply by 0·03937.

III.

THE DISEASE AND ITS REMEDIES.

WHAT is the exact nature of the disease caused by a root-inhabiting *Tylenchus*? How does it spread from one plant to another, and from infected to non-infected lands? Is there any cure or preventive? These are the questions to be answered in the present section. In the two previous sections the subject has been dealt with rather after the manner of a scientific treatise. Such a course needs, however, no apology, for it will now be seen that all the remedies for, and precautions against, this root disease depend completely upon a scientific knowledge of the microscopic worm which is its sole cause.

The nature of the disease caused by *Tylenchus arenarius* will become clear as soon as the diseased tissues are carefully examined. Fig. 7 represents a portion of a diseased parsnip rootlet, considerably magnified. The two swellings have been caused by, and contain, the gall-worms. Between the swellings the rootlet retains its normal size and structure, except that some modification may occur through sympathy with the diseased part. If a thin section of the undiseased part be examined, it will be found to present the usual structure. Beneath the epidermis of the rootlet lie cells constituting the hypoderm, and in the midst of these is found a single large central vascular bundle surrounded by pericambium. The tissue of the central vascular bundle is made up of three portions,—the woody portion or xylom, having in the section the contour of an hour-glass or dumb-bell; the sieve tissue or phloëm, appearing in the section as two narrow crescent-shaped areas, lying between the two parts of the xylom and the surrounding pericambium; the cambium occupying the remaining space, i.e., the two angles where the two xylom portions come into contact near the centre of the rootlet. If now a section of the diseased part of the same rootlet be examined, it will be found that the additional size is caused by an increase in the amount of each tissue, but particularly of those constituting the vascular bundle. The epidermis and hypoderm remain comparatively unaltered in structure, but have increased somewhat in amount. The central vascular tissue, on the other hand, is much altered. It is increased in quantity, and the vessels have become much distorted. Instead of continuing parallel to the axis of the rootlet, as they would normally do, the vessels have become twisted about, and are often found turned to one side or the other, passing sometimes in a radial direction, and even in some cases turning backward. Whatever portion of the tissue has been actually invaded by the worm is easily recognized by its yellow colour. In the majority of cases, according to my observations, it is the cambium of the rootlet that suffers the greatest destruction.

The rootlets are the most fundamental organs of a land-plant. Upon them depends its supply of water and earthy material. Taking this fact into consideration, we shall no longer wonder after noting the changes wrought by the gall-worm, why so small an assailant can do so great injury. The plant is attacked at its weakest point. The tissues of one of its most

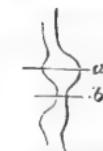


FIG. 7. PORTION
OF A ROOTLET OF PARSNIP.
Showing two galls due
to attack of gall-worms;
magnified.

essential sets of organs, the rootlets, become aborted. The absolutely essential food due the plant from the soil is cut off, and unable to live upon air alone it dies.

Let us now turn to the disease as manifested in the potato. Fig. 8 represents more or less spherical growths which appear in the substance of attacked potatoes. These growths seem always to be connected with distorted vascular tissue. They are found to vary much in size, and there seems little doubt that the "knobs," characteristic of the disease as it appears on the potato, are the result of these small beginnings. Each such body is composed of a thick outer wall, and an inner granular mass.



FIG. 8. TISSUE OF POTATO.

a, cell containing starch grains; b, spherical growth seen in attacked potato; c, vesicular tissues x 40.

These appearances in the parsnip and potato lead me to suspect that the abnormal growths caused by *Tylenchus arenarius* are probably to be compared to the galls produced on leaves by various insects. It is well known that leafgalls are caused in the first place by a disturbance of the vascular tissues. The gall-producing insect commonly pierces a vein of the leaf with its ovipositor when depositing its egg. It is a common belief that the gall appears in consequence of a fluid injected by the insect at the time of laying the egg. I do not know whether this belief is supported by any good evidence. Possibly the mere irritation of such a foreign body as the egg of an insect or the wriggling larva hatched from it may be sufficient to account for the growth of the gall. Certainly there are difficulties in explaining the growth caused by *Tylenchus* on the theory of the irritation being caused by an excretion. The more natural explanation seems to be that the abnormal growths are the result of mechanical irritation.

If I am right in comparing the swellings produced by *Tylenchus arenarius* to the leaf-galls produced by insects, then the former should be called root-galls, and the *Tylenchus* itself may appropriately bear the name of the gall-worm. Dr. Neal has called the disease, as it appears in the United States, the root-knot disease. His name can have no reference to knots, the places where branches originate, otherwise it would be entirely inappropriate, but refers to the characteristic appearance produced by the disease on rootlets, which has been compared to the appearance of a thread with knots tied in it. The German name for the disease caused by *Tylenchus Schachtii* is Rübenmündigkeit—that is, turnip-lassitude or beetroot-lassitude, referring to the tardy growth of the diseased plants. I believe both these names will be supplanted by the simple term "root-gall" (Wurzelgalle), which may be thus defined—abnormal growths on roots and rootlets, caused by the attacks of gall-worms.

Historical.

It is not until within recent years that we have arrived at an accurate knowledge of the habits of the gall-worm, although the disease root-gall has been known for a very long time. How long root-gall has been recognized as a distinct disease of the sugar-beet of Europe I am unable to say, but that it is very many years is certain. The root-gall of the peach has, according to Dr. Neal's exceedingly useful pamphlet, been known to the white people of the South Atlantic and Gulf States of America since the earliest settlement of the country; and, according to the same authority, reliable agriculturists state that the disease is indigenous there, they having seen it in places where neither trees nor plants had ever been introduced

from other sections. The disease is now known to occur in North America on a belt of land 150 miles wide, extending from Texas along the Gulf of Mexico and Atlantic coast northward to the January isothermal of 50° Fah. According to the best testimony yet obtained, the peach tree formerly grew on this area with no other disease than the borer, except in damp localities, while now in many places, owing to the prevalence of root-gall, the trees that do well are the exception. This fact shows how the disease has spread, or at least increased, and should serve as a warning to Australians.

In the United States the plants that have been found to be attacked by *Tylenchus arenarius*, the Australian worm, are as follows:—

Badly affected.—Roots of cabbage, kale, potato, banana, radish, okra, pea, peanut, cow-pea, bean, squash, pumpkin, melon, cucumber, tomato, beet, plum, apricot, peach, almond, fig, English walnut, willow, gourd, bigonia, sunflower, amaranth, dahlia, koniga, iberis, coleus, achyranthes, purslane, sand-purslane, verbesina, worm-wood, Jerusalem-oak.

Slightly affected.—Roots of cotton, egg-plant, pepper, spinach, cassava, maize, orange, grape, mulberry, walnut, pecan, hibiscus, ice-plant, parlor ivy, morning-glory, nolana, petunia, boussingaultia, spirea, flowering almond, buddleia, cape jessamine, shepherd's purse, blackberry, dewberry, eupatorium, cypress vine.

These lists include the majority of the most useful food-plants, many ornamental plants, and a number of the commonest weeds. Among the latter, the roots of purslane, amaranth, Jerusalem-oak, and worm-wood, harbour the greatest number of worms.

The extent of the damage done by gall-worms is difficult to estimate. Much land in Europe has become so badly infested that certain crops—for example, sugar-beet—have had to be abandoned altogether. Not a beet-root will mature. The plants break the ground, languish a few weeks, and then die. Since time immemorial, crops of various kinds have died suddenly—so suddenly, Dr. Neal remarks, as to justify the expression, “struck by lightning.” The unknown cause in some such cases has probably been the gall-worm. Many an agricultural or horticultural failure attributed to the use of improper fertilizer, to poor soil, or wrong cultivation, has been due to this insidious foe attacking the very fountain-head of vegetation. Were it possible to sum up in pounds, shillings, and pence the damage done either by *T. arenarius* or *Schachtii*, the total would probably amount to a fortune for a nation.

Remedies.

All that can be done in combating root-gall must be directed toward prevention. Once the gall-worm gains access to the roots, the game is up. A leaf-destroying pest may be dealt with even after its attack has made some progress, but thus far, at least, roots and rootlets are inaccessible except at the expense of the life of the plant. Hence it follows that all rational remedies for root-gall must be directed either toward ridding the soil of the gall-worms, or toward putting such obstacles in their way, or so reducing their number, as to render their ravages bearable. These ends have been sought in various ways:—

1. By the use of some chemical, preferably a fertilizer, which will destroy the free-living larvae.
2. By the selection of varieties not subject to root-gall.
3. By trapping the worms and thus removing them mechanically from the soil.

I shall consider the last of these methods first.

1. *Trapping*.—It consists in actually capturing the worms and then killing them by hand or by machinery. How to capture a foe numbering millions and doubly masked by being invisible and being hidden away underground might well seem a puzzling question. How it was answered constitutes one of the interesting passages in the history of applied science. The gall-worm of the sugar-beet had long been known to be one of the worst pests of that crop. Various investigations were made and various remedies tried by those interested in the sugar-beet industry, but to little purpose. Year by year the pest grew worse,—more and more land had annually to be abandoned by the beet grower. At this point the philosophical faculty of the University at Leipzig offered a prize for the best investigation of the cause of the Rübenmündigkeit. The prize was awarded to Strubell for an investigation whose results are detailed on page 170, under the head of *T. schachttii*.

Professor Kühn, making Strubell's investigations the basis of his reasoning, now devised a plan for trapping the larvae. Noting that, according to Strubell's investigations, the larvae on entering the young beet plant became mature in about five or six weeks, he predicted that if the plants were pulled at the end of four weeks, the worms in them would die without producing a new brood. It will be seen that Professor Kühn's plan was based on a careful perusal of the life-history of the *Tylenchus*. If the plant should be allowed to remain five weeks before being pulled, the worms would, it is true, be killed, but *not so the eggs which in five weeks the females would have produced*. These eggs would ultimately hatch and the pest continue. But after precisely four weeks, even the oldest worms in the roots would not yet have produced eggs, and, being at that time motionless sacs, incapable of boring their way out, must perish from starvation if the host-plant should suddenly die. In other words, Kühn proposed to make traps of the young plants, and naturally chose such plants as are loved best by the worms. Sugar-beet was selected as the plant likely to entrap the greatest numbers.

The result of the experiments based upon Kühn's plans was a brilliant one. A piece of ground, so badly infested as to be useless to the sugar-beet grower, was sown with sugar-beet. After four weeks the plants were pulled, and another lot of seed sown. The experiment was repeated a third time, if necessary, and it was then found that the pest was controlled. The time occupied was about three months. The plants whose roots were used as traps could be turned to account as fodder or fertilizer, so that the twelve weeks were not a dead loss. In Kühn's first experiments the plants were pulled by hand. That operation was expensive, and led to a trial of ploughing up the trap-roots, and this plan was found to answer almost equally well.

It is beforehand to be supposed that the Australian *T. arenarius* may be trapped in the same way as *T. schachttii*, but the time required for its development is not yet accurately known. As Consulting Pathologist to the Agricultural Department, it is understood that only my spare time is available, and that has latterly been so very meagre that since first giving attention to this matter, one month since, I have found but three days in which to make it the subject of investigations. In consequence, I have no data for giving the *precise* length of time required for the larva to mature in roots. The most I can say is that it is probably less than that required by the sugar-beet gall-worm. Consequently, in any trial of Kühn's remedy in dealing with *T. arenarius*, it will be best, in the present state of our knowledge, to keep well within his limits and allow (say) three weeks before ploughing up

the trap-roots. Mangels will make the best trap-root, and they should be sown thickly.

2. *Gall-proof Varieties.*—Dr. Neal recommends, as a practically gall-proof stock for the orange, the hardy bitter-sweet or sour species, and, with some qualification, *Citrus trifoliata*, and the Japanese Unshin, or Satsuma; as a nearly gall-proof stock for the peach, seedling American wild plum or one of the Japanese plums Kelsey, Satsuma, or Ogru; as a stock for grapes perhaps the *cordifolia* or *rufipina* races. For other plants subject to root-gall he found no resistant stocks.

Fire is a powerful destructive agent which may, in certain cases, be brought into play in combating root-gall. The larvæ of the gall-worm infest the soil to a depth of at least 2 feet, but by far the greater number are found within a few inches of the surface. The heat of a large fire will penetrate to this depth in sufficient degree to destroy life. This fact may be applied in setting out those trees particularly subject to root-gall, such as the peach, apricot, almond, plum, and fig. Nothing short of a large fire, lasting several hours, will kill the worms. The tree must be set in the midst of the burnt area, and no soil or fertilizer used except such as is known to be free from gall-worms.

3. *Use of destructive chemicals.*—Experiments looking towards the use of some fertilizer or chemical destructive to gall-worms have been made, and the results may be summed up as on the whole negative. No thorough-going chemical remedy for Rübenmündigkeit has ever been discovered, although multitudes have been tried. Similar negative results were obtained by Dr. Neal in the case of *T. arenarius*. Still the results are interesting, as pointing out what positively will not succeed; furthermore, they may be made the basis of plans for further trials.

Of all the vermicides yet tried, lime receives the highest commendation. It must be used in large quantities to be effective. (The same is true of the muriates and sulphates of potash and ammonium.) One to two tons of lime to the acre, applied, not all at once, but part in Juno and the remainder in October or November, may be recommended. The result is the destruction of a large number of worms; but many eggs, protected by the tissues in which they are being incubated, doubtless escape destruction, and live to propagate the disease. I have noticed that when the disease is combated with chemicals, the method has been in all cases drastic, the attempt being to kill all the worms at one fell swoop. Possibly a homœopathic treatment would be more fatal. It is easy to believe that many of the experiments which have been tried were in reality effective so far as they went, although pronounced unsuccessful because the disease reappeared. My experiments have already shown that the period occupied by the development of the egg of *T. arenarius* may possibly extend over two months or more. While yet in the egg, the young worm is protected by the shell; and this protection is a good one. The shells of nematode eggs (as well as the skin of the larva when it is being cast) are comparatively impenetrable. Poisons which would at other stages of life be fatal, can therefore be withheld by embryos and moulting larvæ. I may support these statements, which are based on my own observations and experiments,* by the remark that the eggs develop in the very midst of decaying matter. The roots attacked by the disease die and decay, thus giving rise to chemicals of considerable strength and activity. Yet the eggs develop unharmed—quite likely, on account of the impenetrability of their shells. Now, suppose in some of the numerous experiments that have

* For instance, I have observed that species which under ordinary circumstances are instantly killed by osmic acid may withstand the acid for an hour when moulting.

been made, all or most of the larvae actually in the soil and unprotected were killed by the poison used. It is plain that the remedy was a good one, thus far; yet, if the eggs and moulting larvæ escaped destruction, because protected by their coverings, they would give rise to galls in the course of a few weeks or months, and the experiment would be pronounced a failure. I therefore repeat my suggestion that perhaps a more gradual and longer-continued treatment would be successful with some of the chemicals already tried and pronounced ineffective. Among those tried are kerosene emulsion; various solutions of arsenic; bisulphide of carbon; carbolic acid; the sulphates of ammonium, potash and iron; the sulphite, sulphide, and muriato of potash; hyposulphite of soda; tobacco dust.

4. *Frost.*—Dr. Neal says that if in places where the soil is frozen to some little depth each year the ground be ploughed at times during the cold season, it is reasonable to suppose that great destruction of the gall-worms will ensue. I know of no experiments demonstrating that the worms will not revive from the effects of low temperature, as they certainly will from those of long continued dryness.

5. *Drainage.*—It has long been known that drainage has an important bearing on the spread of *T. devastatrix*. Currents of water on or beneath the surface of the soil will pick up and transport small and light objects. Those objects of least specific gravity are most subject to the transporting power of water. Of all the constituents of the soil, none probably are more likely to be thus moved from place to place than minute organisms such as the eggs and larvæ of gall-worms; hence the great importance of drainage in connection with root-gall, as well as with the ravages of *T. devastatrix*. By a good system of surface drainage, surface-water may be so controlled as to spread the disease as little as possible. It is needless to go into particulars, as any farmer can easily devise a system of drains suited to his individual case. This matter must not, however, be overlooked by anyone whose land is infested. It is certain that water is one of the chief agents in the spread of root-gall.

6. *Famine.*—Famine is as destructive to gall-worms as to other animals, and there is not the slightest doubt that land kept quite clear of vegetation will, in time, become disinfected—the worms dying of starvation. How long a time would be required is unknown; probably more than a year. It is not likely that land will be given up for such a length of time, especially when it is remembered that it must be kept clear of vegetation at considerable expense; but the fact that the worms may be starved out utterly leads to the question whether or not, by a proper rotation of crops, they may not become so reduced by partial starvation as to become comparatively harmless.

The gall-worm evil, like most evils, is endurable so long as it does not become too great. It is only when the soil swarms with larvæ that serious damage is effected. Now, certain crops—for instance, maize and the cereals generally—are but little affected by root-gall. If land badly infested be planted with maize, it is reasonable to suppose that the effect will be much the same as if it stood idle and bare; but, *no experiments having yet been made*, it is impossible to say what value this method may have. Of course, this plan contemplates keeping the land absolutely free of weeds while it is bearing maize. The tough root of maize is not easily penetrated by the worms, and, finding no other plant to feed upon, they must, it would seem, of necessity starve.

7. *Use of non-infected Soil.*—When trees are to be set in infected land they may be filled in with earth taken from a depth of at least 2 feet. Such

earth is practically free from gall-worms, and, if mixed with some artificial fertilizer known to be also free from them, will be found to answer the purpose well. This is a method recommended by Dr. Neal, though he cautions the gardener to beware using too much nitrogenous fertilizer, saying the vigorous growth thereby promoted is unusually subject to root-gall, because the root tissues are tender and therefore easily penetrated by the worms.

8. *Artificial Barriers.*—Another precaution which is of service in protecting young trees from root-gall is the use of artificial subterranean barriers. Having sterilized a spot of ground for a tree by means of fire, or by the substitution of uninjected subsoil, it becomes a question whether this now uninfested spot cannot in future be kept free from gall-worms, even though the surrounding land be infested. A means towards this end is the placing in the soil of a barrier or obstruction all around each tree, at a distance of (say) 2 feet from it. The barrier may be of staves placed close together in a circle, or, better, of old scraps of iron, such as old kerosene tins or old galvanized sheet-iron. Bark is an excellent and cheap material for the purpose. The barrier should be vertical, or slope from the tree so as to leave room for unobstructed root-growth. The purpose of such a barrier is evident at once. It prevents to a certain extent the entrance of worms from the outside infested soil. It will be effective in proportion as it is tight. Staves would therefore be less effective than old tin or iron in moderately large pieces. The latter, however, are much less likely to be at hand in sufficient quantity. Bark is probably about as available as any material. The pieces of bark should overlap each other. Of whatever material the barrier is made it should extend from a little above the surface of the soil downward at least 18 inches—better, 2 feet. Such an obstruction will, even if made of wood or bark, which will decay in the course of a few years, protect the young tree until it has attained considerable size and sent its roots deep into the ground. After that it is comparatively safe. Old trees with tough roots sinking deep into the ground suffer but little from the gall-worm.

Of course these barriers, even if watertight, will not prevent the entrance of the gall-worms spattered into the enclosed area during rains, or blown in as dust in dry weather. This fact points toward the usefulness of a mulch (uninfested, of course).

How does the root-gall spread, and at what rate? The disease will spread from a centre of infection at the rate of a few rods each year. In such cases its progress is through the soil, and may be marked by its effects on roots. But infection does not always occur in this manner. During a spell of dry weather the eggs and dried up larvæ exposed on the surface of cultivated ground may be whirled aloft by the wind and scattered for miles over adjacent territory. The disease may thus unseen spread by leaps, making itself felt however in the new localities only after some years have elapsed, and the worms have become abundant by natural increase from the few eggs or larvæ deposited by the wind. These facts indicate sufficiently the rate at which root-gall may spread. The facts and rate are much the same as for *T. devastatrix*.

The different modes by which the disease may pass from one piece of land to another deserve careful consideration, for upon them are based a number of useful precautions. Some of these modes have already been mentioned incidentally, but the importance of the subject will justify dwelling upon them at greater length, even at the risk of some repetition. The migrations due to the animal's own muscular powers are not rapid or great. In fact

they are so slight that I think it may be questionable whether they would account for any but the very slowest spread of the disease. Even when the worms pass from plant to plant in the same paddock it is questionable whether the movement is not due to transportation by some of the numerous agencies constantly at work in their neighbourhood. Almost everything that moves either in or upon the soil may transport the minute eggs and larvae of gall-worms. Air, water, animals are all agents in disseminating the disease. The manner in which winds may act has already been alluded to, and some precautions, such as mulching, suggested. Under the head of drainage we have seen how necessary it is in combating root-gall to have an eye to the surface currents which during rains may pick the disease up as it were, and deposit it in mass elsewhere. The action of subterranean water has also been lightly touched upon. The general lay of the land determines largely the nature and direction of the currents in the soil. These doubtless have something to do with the spread of the disease. Here very little can be suggested beyond a proper system of drainage.

One set of agencies in the spread of root-gall, and a most important one too, has not yet received consideration. I refer to other animals. Insects, earth-worms, birds, domestic animals, man himself, are all factors in the life history of the gall-worm. Let the farmer who is fresh from cultivating his infested paddock show me his boot, and the chances are that I shall be able to remove from it small clumps of earth containing larvae of the gall-worm. The hoofs of his horses are in a similar condition. If the weather is damp, it only needs a gun to demonstrate that even the feet of the magpie that followed the plough repeat on a smaller scale the same conditions. The insect that burrows in the ground and brings to the surface subterranean material is active in aiding the gall-worm in finding new pastures. The egg or larva leaves the mandibles of the insect only to be seized up by the wind, or pressed with other matter into some crevice in boot or hoof, and thus, it may be, travel miles before being again set down. This is far from being a fancy sketch; every statement rests on the most unimpeachable observation. Even the hands when soiled from field work may carry enough material to start a thriving colony of gall-worms. It only needs to be washed off, and thrown with the water around the roots of some favourite plant (to help it along, poor thing!), to form the nucleus for a new infested area. But enough has been said on this head to put those interested on their guard. The thorough cleansing of boots and hoofs before passing from infested to uninjected land is too obvious a precaution to need mentioning. There could be no more appropriate closing statement to this section than that of the general principle that whatever moves and comes into contact with the eggs and larvae of gall-worms is likely to afford them the means of finding new victims.

EXPLANATION OF PLATE IV.

The parsnip and potato represented came from Pretty Gully; the remaining figures are after Neal. In all the figures the galls are clearly represented in the form of irregular and often dark-coloured swellings.

1. Peach. (Reduced.)
2. Okra. (Reduced.)
3. Parsnip. (One-half natural size.)
4. Fig. (One-fourth natural size.)
5. Potato. (Natural size.)
6. Weeping-willow. (One-fourth natural size.)
7. Radish. (One-fourth natural size.)
8. Cow-pea. (Reduced.)
9. Grape. (Reduced.)

[One Plate.]

